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A New Genus and Species of Microhylid Frog from the Cerro de la Neblina Region of Venezuela and a Discussion of Relationships Among New World Microhylid Genera

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ABSTRACT

Adelastes hylonomos, new genus and species, is described from specimens collected on the Cerro de la Neblina Expedition of 1984–1985 at a site in lowland rain forest near the base of Cerro de la Neblina at the southern tip of Venezuela. Cladistic analysis of selected traits of morphology, repro-

duction, and vocalization suggests that *Adelastes* and four other genera—*Arcovomer*, *Chiasmocleis*, *Hamptophryne*, and *Syncope*—form a monophyletic group. A preliminary phylogenetic arrangement of these and other American microhylid genera is presented.

RESUMEN

Se describe *Adelastes hylonomos*, un género nuevo y una especie nueva, de ejemplares coleccionados durante la Expedición al Cerro de la Neblina en 1984–1985, en la selva pluvial baja cerca de la base del Cerro de la Neblina, en el extremo meridional de Venezuela. El análisis cladístico

basado en ciertas características de morfología, reproducción y vocalización sugiere que *Adelastes* y otro cuatro géneros—*Arcovomer*, *Chiasmocleis*, *Hamptophryne*, y *Syncope*—forman un grupo monofilético. Se ofrece un arreglo preliminar de estos y otros géneros microhílidos americanos.

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INTRODUCTION

The chief purpose of the Cerro de la Neblina Expedition of 1984–1985 was to sample broadly and intensively the flora and fauna of a little known region of southern Venezuela. The massif of Cerro de la Neblina, rising abruptly out of the lowland rain forest to over 3000 m elevation, was the focus of the Expedition, but participants carried on extensive work in the lowlands at the base of the massif as well. The elevation and isolation of Cerro de la Neblina coupled with the lack of previous herpetological investigation virtually assured that undescribed forms

would be found on that mountain. The diversity of the Amazonian biota and the state of knowledge being what they are, novelties were expected in the lowlands too, though the discovery of an undescribed species of microhylid frog that represented a new genus as well as scarcely predictable. The purpose of this contribution is to describe the new taxa and to discuss relationships among American microhylid genera. A general account of the expedition as well as a comprehensive account of the herpetological collections are expected from other authors.

ACKNOWLEDGMENTS

The Cerro de la Neblina Expedition was organized in Venezuela by the Fundación para el Desarrollo de las Ciencias Físicas, Matemáticas y Naturales (Dr. Francisco Carrillo Batalla, President), under the sponsorship of the Ministerio de Educación, the Consejo Nacional de Investigaciones Científicas y Tecnológicas, and the Instituto Nacional de Parques. Dr. Charles Brewer-Carías served as coordinator and expedition leader. Support from the William H. Phelps Fund and a grant by the National Science Foundation made possible the participation by staff and students from the American Museum of Natural History.

I acknowledge with thanks the opportunity to participate in this expedition afforded by the individuals and institutions mentioned above. Drs. Charles J. Cole and Roy W. McDiarmid were good-natured, tolerant field companions who made essential contributions to this study. Frances W. Zweifel, as always, helped greatly with preparing the illustrations. Technical assistance of Norma M. Feinberg (X-ray photographs) and Carol Townsend (clearing and staining) is gratefully acknowledged. Drs. David Cannatella, Roy W. McDiarmid, and William F. Pyburn helpfully criticized the manuscript. Drs. Richard J. Wassersug and William F. Pyburn kindly furnished a copy of their manuscript on *Otophryne*. Janis Roze translated the abstract.

METHODS

I measured preserved specimens either with dial calipers read to the closest 0.1 mm or, when appropriate, used an ocular micrometer in a dissecting microscope read to the closest 0.05 mm. Measurements (abbreviations in parentheses) were taken as follows: length from snout to vent, tip of snout to cloacal opening (SV); head width at widest point, generally at the angle of the jaws (HW); head length, tip of snout to rear edge of tympanic annulus (HL); tibia length, between heel and outer surface of flexed knee (TL); hand length, between proximal edge of inner metacarpal elevation and tip of third finger (Hand); foot length, between proximal edge of inner metatarsal elevation and tip of fourth toe (Foot); eye or orbit length, between anterior and posterior edges or corners of eye opening (Eye); distance between anterior edge of eye opening and center of external naris (EN); distance between centers of external nares (IN).

Sex was determined by examination of gonads.

Osteological material included specimens cleared and stained for bone and in most instances cartilage (Dingerkus and Uhler, 1977), supplemented by X-ray photographs and dissection of preserved specimens in the collection of the American Museum of Natural History. Skeletal material used and species examined by X-ray are listed near the end of the paper.

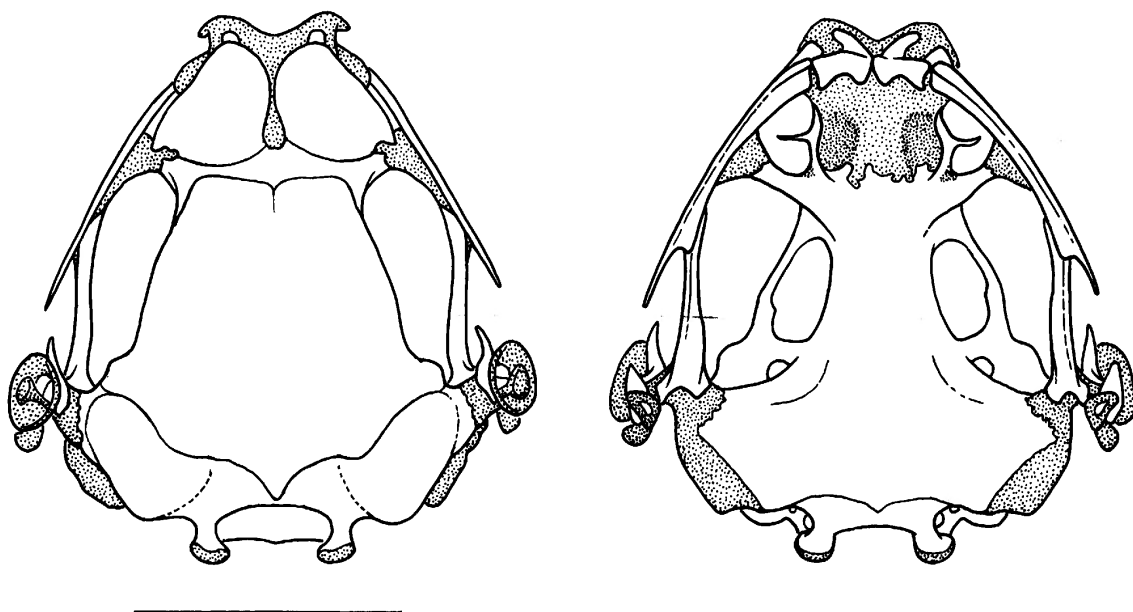


Fig. 1. Dorsal (left) and ventral views of the skull of *Adelastes hylonomos* (AMNH 123697). Stippled areas are cartilage, clear areas bone. Scale line spans 4 mm.

Tape recordings were analyzed on a Kay Model 7800 Sona-Graph.

The following abbreviations identify museum catalog numbers: AMNH, American Museum of Natural History, New York; MBUCV, Universidad Central, Caracas, Venezuela; USNM, National Museum of Natural History, Washington, D.C. Personal field catalog abbreviations are: JC, Charles J. Cole; RWM, Roy W. McDiarmid; RZ, Richard G. Zweifel.

DESCRIPTION

Adelastes, new genus

TYPE SPECIES: *Adelastes hylonomos*, new species.

CONTENT: The genus is monotypic.

DIAGNOSIS: A genus of the family Microhylidae (palatal ridges present, mentomandibular bone with a cartilaginous extension, pectoral girdle firmisternal) and subfamily Microhylinae (toothless, diplasiocoelous, prevomers reduced) apparently unique within the family—and possibly among all frogs—in that the anteromedial part of the body of the hyoid apparatus consists of a discrete bony plate posterior to the hyoglossal sinus (fig. 2). Other microhylid genera may show consid-

erable calcification of the hyoid (e.g., *Ela-chistocleis*), but none is known with a clearly defined area of bone. Single (*Leiopelma*) or paired (*Bombina*) parahyoid bones occur in other genera (Trewavas, 1933; Trueb, 1973, fig. 7) but do not border on the hyoglossal sinus. (Readers comparing fig. 2 with the illustrations in Trueb should not confuse the clear area representing bone in fig. 2 with areas of similar appearance in Trueb's drawings which represent hyoglossal membranes.)

Adelastes lacks clavicles, procoracoids, and palatine bones, and in the key furnished by Carvalho (1954) runs down to the couplet containing the genera *Synapturanus* and *Myersiella*. Comparisons with these and other genera are in a subsequent section.

ETYMOLOGY: The generic name derives from the Greek words *adelos*, meaning concealed, and *astes*, a singer, and is of masculine gender.

OSTEOLOGY: This description is based on a single adult male specimen, SV 27.6 mm, cleared and stained for bone and cartilage with Alizarin Red S and Alcian Blue. The skull is unusually well ossified, with large nasal bones almost in contact with one another and with the frontoparietals fused into a single bone (fig. 1). The alary process of the pre-

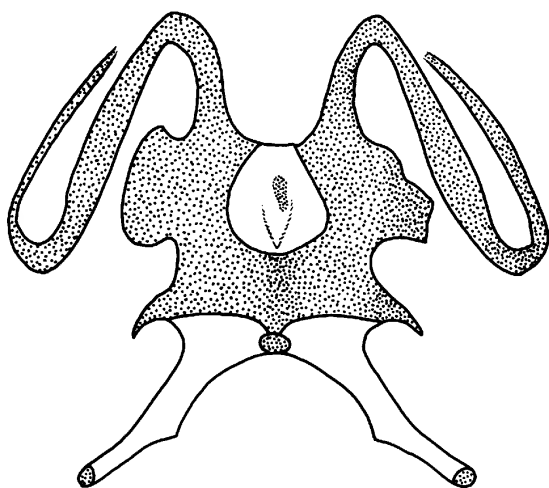


Fig. 2. Hyoid apparatus of *Adelastes hylonomos* (AMNH 123697) in ventral view. Stippled areas are cartilage; clear areas bone. Scale line spans 6 mm.

maxilla is nearly vertical and the premaxillary shelf is moderately indented posteriorly (fig. 10E). The premaxilla and maxilla lack teeth. The maxilla tapers posteriorly and does not contact the quadratojugal. An arm of the prevomer extends laterally along the front edge of the internal naris, while the posterior end of the prevomer contacts and fuses with the sphenethmoid (fig. 10E). This last bone forms most of the posterior edge of the internal naris and is exposed dorsally between the nasals and the frontoparietal. I cannot distinguish the ventral hiatus usually seen in the sphenethmoid of microhylids. No palatine bone is evident. The anterior end of the parasphenoid passes indistinguishably into the sphenethmoid. The otoccipital region is moderately well ossified except for the cartilaginous crista parotica (fig. 1). The top of the squamosal tilts slightly forward and bears short zygomatic and otic rami.

Fusion of the frontoparietals is unusual. In all other American microhylids examined (see list of specimens studied), the division between right and left elements is conspicuous, both in cleared and stained preparations and in X-ray photographs. In *Adelastes* I can see only a slight trace of separation anteriorly. The posterior border of the frontoparietal is difficult to define due to underlying ossifi-

cation and probably is not shown exactly in the illustration.

The hyoid apparatus (fig. 2) is conventional except for the inclusion of a central bony area (parahyoid) with a free border on the hyoglossal sinus. This bone has a median ridge posteriorly and incorporates a small, irregular area of cartilage. The bone has the appearance of an integral part of the hyoid plate rather than of bone resting on the hyoid plate.

No traces of clavicles or procoracoid cartilages exist. The scapula and coracoid have a bony fusion. The sternum is cartilaginous with no calcification (fig. 9).

The ultimate phalanges taper to narrow, rounded tips.

The eight presacral vertebrae are nonimbricate except for narrow, mid-dorsal projections of the first and second. The eighth vertebra is biconcave and the diaphophyses angle sharply forward (fig. 11B). The sacrum has moderately expanded diaphophyses and a free, bicondylar articulation with the coccyx, which lacks diaphophyses, having only very slight shelflike lateral projections.

The following species description incorporates additional information on morphology.

Adelastes hylonomos, new species

Figure 3

HOLOTYPE: AMNH 123696 (field number RZ 12184), adult male, collected on February 27, 1984, by Charles J. Cole and Richard G. Zweifel near the Neblina Base Camp on the Rio Baria, 140 m elevation, 00°49'50"N, 66°09'40"W, Rio Negro Department, Amazonas Federal Territory, Venezuela.

PARATYPES: MBUCV 6185, 6186, 6187, (JC 4755, 4760; RWM 17320), AMNH 123697 (JC 4761, cleared and stained), USNM 258153 (RWM 17321), collected at the type locality on February 27 (MBUCV 6185) and 28, 1984 (MBUCV 6186, 6187; AMNH 123697; USNM 258153), by C. J. Cole, Roy W. McDiarmid, and R. G. Zweifel, and USNM 258154 (RWM 18022) taken by Reginald B. Cocroft on February 24, 1985, near the type locality.

ETYMOLOGY: The Greek adjective *hylonomos* means forest dwelling.

DIAGNOSIS: As the only member of its ge-

nus, this species is best recognized by the characters of internal anatomy given in the generic diagnosis. Without recourse to examination of the skeleton, the following combination of characters should distinguish *Adelastes hylonomos* from all other American microhylids: dorsum uniform dark brown, venter paler, no color pattern present; normal complement of four fingers and five toes, all well developed and without webbing or fringes; size moderately small, adult males 24–29 mm SV (females not known).

Some markings—dorsal, ventral, or both—are present in almost all American microhylids. *Glossostoma aterrimum* is dark and patternless, but is much larger than *A. hylonomos* and has webbed toes.

Adelastes is similar in external morphology to some *Chiasmocleis*, and I have considered the possibility that it may already have been described in that genus. This does not appear to be the case, for most original descriptions of *Chiasmocleis* species or their synonyms mention or illustrate the clavicle (verified by me for types in the AMNH collection), and all species have characters of color pattern or morphology that distinguish them. *Chiasmocleis hudsoni* Parker, which was found at and near the Neblina Base Camp, although not microsympatrically with *A. hylonomos*, resembles the latter in size, habitus, and pigmentation. It is readily distinguished in having distinctly expanded toe discs with a groove delimiting the anterior and lateral margins of the pad, a patterned venter, and an indistinct light line on the canthus rostralis.

DESCRIPTION OF HOLOTYPE: Adult male with the following measurements (in mm) and proportions: SV 28.9, HW 8.8, HL 8.1, TL 10.0, Eye 2.15, EN 2.3, IN 2.25, Hand 5.7, Foot 11.0; HW/SV 0.304, HL/SV 0.28, TL/SV 0.346, Eye/SV 0.074, EN/SV 0.079, IN/SV 0.078, IN/EN 1.02, Hand/SV 0.197, Foot/SV 0.381.

Head narrow and relatively long (fig. 7E), snout tapering to a sharply rounded tip that projects beyond the mouth; canthus rostralis rounded, not in the least angular, loreal region inclined slightly outward; nostrils dorsolateral, about equidistant from each other and from the eyes, readily visible from above; eyes lateral, diameter about equal to distance to naris, considerably shorter than snout, dis-

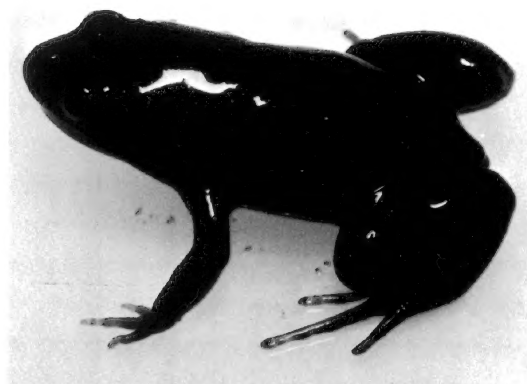


Fig. 3. Paratype of *Adelastes hylonomos* (MBUCV 6185), SV 24.6 mm.

tance between eyelids about twice the width of an eyelid; tympanum not externally evident; body scarcely wider than head; skin smooth with no conspicuous glands or rugosity. Pupil not observed in life, but judged from preserved specimens to be a horizontal ellipse.

Relative lengths of fingers $3 > 4 > 2 > 1$, first more than half length of second; tips rounded to slightly tapered, a little flattened and without terminal grooves; no webbing; subarticular tubercles scarcely indicated but a conspicuous inner metacarpal elevation present (fig. 4).

Relative lengths of toes $4 > 3 > 5 > 2 > 1$, tips flattened into discs scarcely if at all broader than penultimate phalanges, terminal grooves lacking so pad area not well defined; no webbing; subarticular tubercles low, inconspicuous; inner metatarsal tubercle low, rounded; no outer metatarsal tubercle (fig. 4).

In preservative, the dorsal surfaces are dark purplish brown, unpatterned, the hands and fingers slightly paler, the side of face somewhat darker. The ventral surfaces are lighter brown and unpatterned, without sharp demarcation from dorsum. In life the frog was dark brown above with no pattern and gray beneath, also unpatterned, with the throat slightly browner. The iris was black.

VARIATION IN THE TYPE SERIES: Except for minor differences in proportions, the description of the holotype could stand for the six male paratypes as well. Size ranges from 24.6 to 28.9 mm SV, $N = 7$. Proportions are as

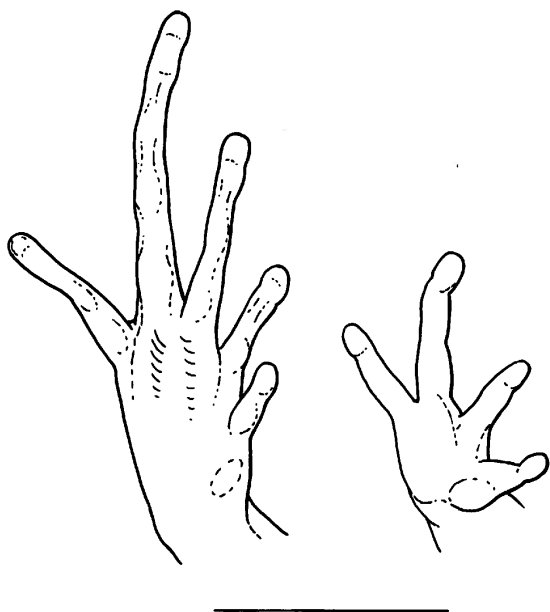


Fig. 4. Underside of right foot (left) and right hand of holotype of *Adelastes hylonomos* (AMNH 123696). Scale line spans 5 mm.

follows (mean, standard error of mean, and range): HW/SV 0.319 ± 0.005 (0.304–0.345); HL/SV 0.290 ± 0.005 (0.271–0.303); TL/SV 0.374 ± 0.007 (0.346–0.401); Eye/SV 0.081 ± 0.002 (0.074–0.086); EN/SV 0.085 ± 0.001 (0.079–0.088); IN/SV 0.083 ± 0.001 (0.078–0.086); IN/EN 1.03 ± 0.005 (1.02–1.05); Hand/SV 0.210 ± 0.003 (0.197–0.224); Foot/SV 0.412 ± 0.009 (0.381–0.443).

HABITAT AND HABITS: The type locality is in rain forest at an elevation of about 140 m. A shallow, sand-bottomed stream, little more than 2 m wide at the time of our visits, wanders among the bottomland trees, where debris lodged above the water level of small, isolated pools testifies to flooding. Calls issuing from the leaf litter at or after dusk led us to all the *Adelastes* we captured or saw. The frogs were not deep within the litter, but were always well enough hidden that they could not be seen without removing some cover. Calling sites did not bear a consistently close relationship to surface water. One frog was uncovered only a few centimeters from a pool into which it escaped, but others were several meters from water. However, we heard no *Adelastes* in forest areas at any great dis-

tance from surface water. The only other locality where I heard *Adelastes* (but did not capture it) was similar to the type locality. Mr. Cocroft found one near the type locality in the midst of a pile of leaves beside a stream.

Other frogs found on the forest floor at the type locality include *Colostethus* sp., *Leptodactylus wagneri* (Peters), *Bufo typhonius* (Linnaeus), and *Synapturanus salseri* Pyburn. None of these occupies precisely the same microhabitat as *Adelastes*: *Colostethus* and the *Bufo* operate diurnally on the surface of the leaf litter; the *Leptodactylus* is riparian; *Synapturanus* calls from the ground deep beneath the litter. Associated species where Mr. Cocroft found his specimen included *Rana palmipes* Spix in the stream, *Leptodactylus riveroi* Heyer and Pyburn on the stream bank, and *Adenomera andreae* Müller in the streamside leaf litter.

We saw no larvae in the waters at the type locality and found no female frogs, so breeding habits are unknown.

CALL: The advertisement call of *Adelastes* is a series of harsh chirps (fig. 5). Among the calls of four individuals tape recorded, there are from 6 to 19 notes in a call with call length varying from 1.2 to 3.5 sec (table 1). The number of notes per second ranges from 3.5 to 5.7. The initial note in a call is about 0.02 sec long; subsequent notes are longer, building up to a typical duration of 0.04 sec for the majority in any one call. There is no clear dominant frequency; most of the energy is between 2000 and 3000 Hz. The temporal pattern of calling is not rigid: anywhere from a few seconds to a minute or more may pass between calls of one frog. We heard *Adelastes* calling at dusk and later in the evening (never in daylight), usually during or following rain.

COMPARISONS WITH OTHER NEW WORLD GENERA

This section treats features, mainly morphological, of *Adelastes* in comparison with those of other genera. The primitive vs. derived states of selected characters are discussed as a basis for assessing relationships.

EXTERNAL MORPHOLOGY

American microhylids, like those in other parts of the world, are morphologically di-

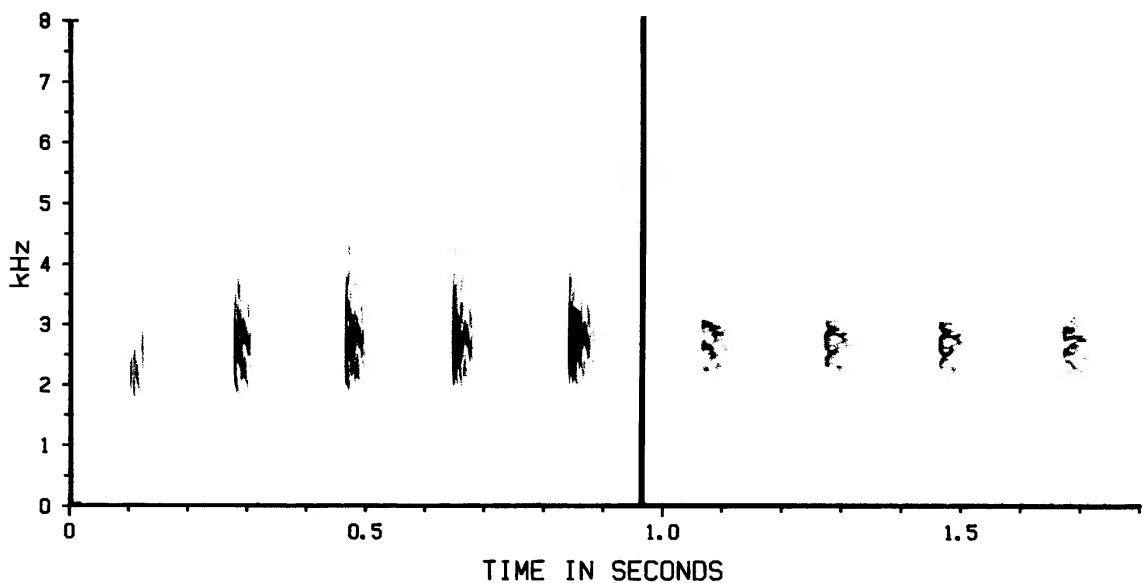


Fig. 5. Audiospectrogram of one complete call of holotype of *Adelastes hylonomos* (AMNH 123696), recorded February 27, 1984, substratum temperature 25.2°C. First five notes graphed with 300 Hz filter, remaining four with 45 Hz filter.

verse. They range in adult size from less than 12 mm snout-vent length (*Syncope*) to more than 60 mm (*Dermatonotus*, *Glossostoma*). There are species with tiny heads on rotund bodies (e.g., *Dasypops*, *Synapturanus*), broad-headed forms (*Ctenophryne*, *Stereocyclops*), and all degrees of snout shape (figs. 6, 7). Eye size also varies (figs. 6, 7). In a small sample representing all genera except *Hyophryne*, Eye/SV ranges from 0.042 to 0.123. In these morphological characteristics *Adelastes* is very much an average frog, avoiding the extremes seen in some genera. I have not subdivided these aspects of body shape into polarized characters. If confronted with only *Dasypops* and *Glossostoma*, for example, one

could assign the more primitive position to the latter with little dispute, but when the intervening spectrum is considered decisions become too arbitrary.

A small majority of American genera (and some Asiatic microhylines as well) exhibit a transverse fold of skin, the occipital fold, just posterior to the eyes (fig. 6), though this character is not equally distinct in all individual specimens. *Adelastes* and five other genera lack this fold (figs. 6, 7). On the tenuous bases of communality and its presence in otherwise presumably primitive genera, I regard the presence of the fold as primitive and its absence derived.

The ear region is covered by undifferen-

TABLE 1
Call Statistics for *Adelastes hylonomos*

| Specimen | Duration, sec | Notes/call | Notes/sec | Temp, °C | N | AMNH tape no. |
|--------------------------|------------------|--------------|---------------|----------|----|---------------|
| AMNH 123696 ^a | 1.76 (1.21–2.11) | 9.1 (6–11) | 4.7 (3.5–5.1) | 25.2 | 7 | 249 |
| No voucher ^b | 2.22 (1.77–2.90) | 13.2 (11–17) | 5.6 (5.4–5.7) | 25.2 | 11 | 249 |
| No voucher ^c | 2.05 (1.86–2.20) | 12.0 (11–13) | 5.5 (5.4–5.5) | 24.9 | 4 | 250 |
| USNM 258154 ^d | 3.24 (2.91–3.55) | 17.0 (15–19) | 5.0 (4.8–5.1) | 24.4 | 4 | 250 |

^a Recorded by R. Zweifel and C. J. Cole, Feb. 27, 1984.

^b Recorded by Zweifel, Cole, and R. McDiarmid, Feb. 28, 1984.

^c Recorded by Zweifel, March 9, 1984.

^d Recorded by R. Cocroft, Feb. 24, 1985.

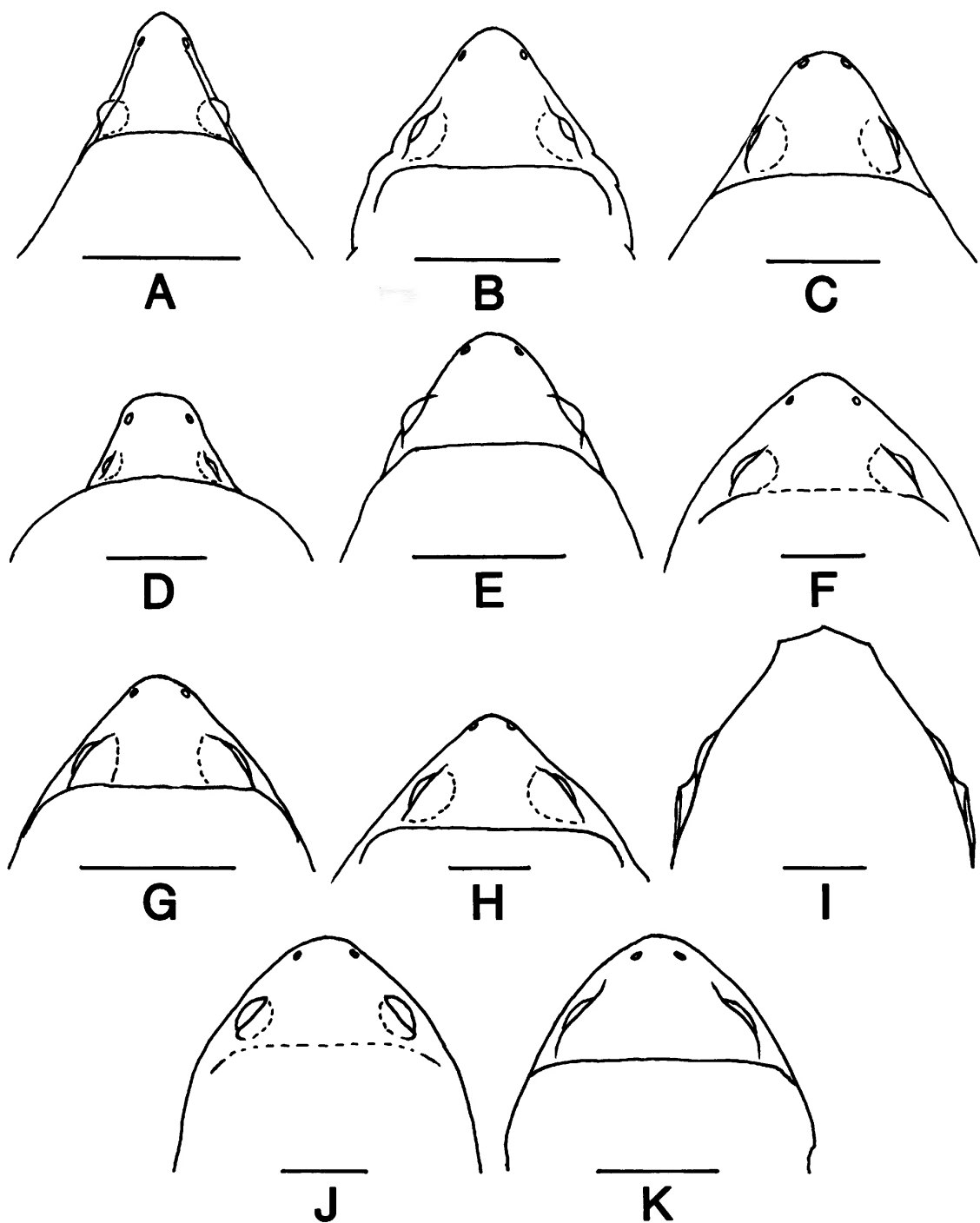


Fig. 6. Heads of microhylid frogs in dorsal view. The bottom edge of each drawing is at the anterior edge of the forelimbs. Scale lines each represent 5 mm. **A.** *Synapturanus salseri*. **B.** *Myersiella microps*. **C.** *Elachistocleis ovalis*. **D.** *Dasypops schirchi*. **E.** *Gastrophryne carolinensis*. **F.** *Ctenophryne geayi*. **G.** *Hypopachus variolosus*. **H.** *Dermatonotus muelleri*. **I.** *Otophryne robusta*. **J.** *Stereocyclops incrassatus*. **K.** *Glossostoma aequatoriale*.

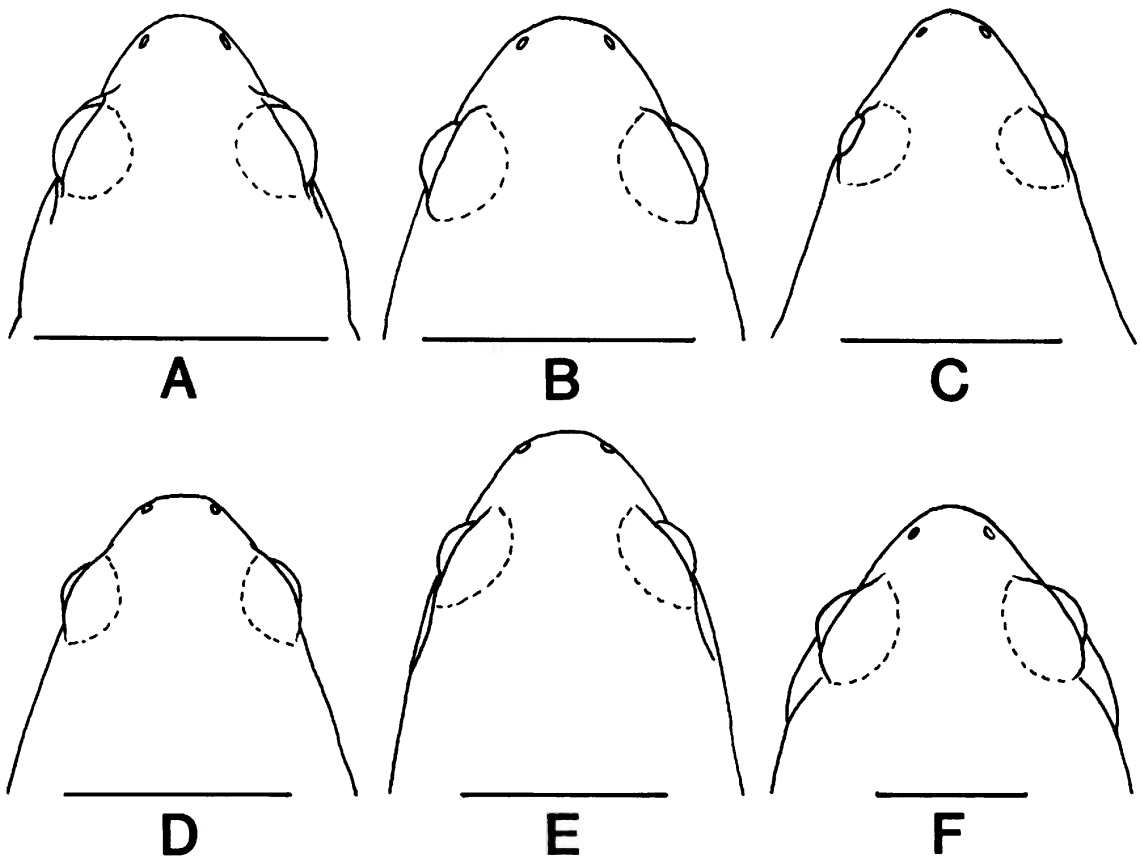


Fig. 7. Heads of microhylid frogs in dorsal view, presentation as in figure 6. A. *Syncope* sp. B. *Chiasmocleis hudsoni*. C. *Chiasmocleis panamensis*. D. *Arcovomer passarellii*. E. *Adelastes hylonomos*. F. *Hamptophryne boliviana*.

tiated skin in most American microhylids, with the tympanic annulus scarcely if at all visible. Only *Otophryne* has a large tympanum conspicuous externally—slightly larger than the eye in two males I examined and slightly smaller in one female. The only other American genus with the tympanum externally differentiated is *Syncope*. It is distinct and nearly half the diameter of the eye in *S. antenori* (Walker, 1973), but is hidden in the other species of the genus, *S. carvalhoi* (Nelson, 1975).

Leg length is only moderately variable in American microhylids. My sample of all genera except *Hyophryne* has a grand range of 0.304–0.505 TL/SV. Again, *Adelastes* is close to the midpoint (mean 0.374).

The amount of toe webbing varies among

genera and within the most speciose genus, *Chiasmocleis*. In addition, sexual dimorphism and temporal variation associated with breeding season may influence this character. *Chiasmocleis* shows a complete spectrum from no webbing at all to virtual full webbing. All genera considered, more than 75 percent of the species show no webbing (*Adelastes* included) or only a basal trace. *Arcovomer* lacks webbing and is peculiar in having rows of spinules on the edges of the toes. *Hypopachus variolosus*, a species with moderate webbing, has similar spinules on the margin of the web.

The tips of the toes may be small and rounded, flattened and broadened with a terminal groove, or some stage between. The first of these conditions, which is the simplest

and most widespread, may be the primitive one. It is seen in some *Chiasmocleis* and in *Dasylops*, *Dermatonotus*, *Elachistocleis*, *Gastrophryne*, *Glossostoma*, *Hamptophryne*, *Hypopachus*, *Myersiella*, and *Stereocyclops*. The other extreme occurs in at least one *Chiasmocleis*, whereas other *Chiasmocleis* and the following genera exhibit various degrees of flattening with little or no expansion, and terminal grooves indistinct or absent: *Adelastes*, *Arcovomer*, *Ctenophryne*, *Hyophryne*, *Otophryne*, *Synapturanus*, and *Syncope*.

The condition of the subarticular tubercles tends to parallel that of the toe tips. Species with small, rounded tips generally have more prominent tubercles than those with flattened tips. *Chiasmocleis* again shows a range of states, from tubercles barely evident to fairly prominent. *Adelastes* is at the presumably derived pole, with low, rounded tubercles. Development of the inner metatarsal tubercle agrees with that of the subarticular tubercles. *Hypopachus* is special in that this tubercle is enlarged into a projecting digging tool, and an outer metatarsal tubercle also is present. A distinct outer tubercle exists otherwise only in *Gastrophryne usta*.

One genus, *Syncope*, is unique in having only three fingers free, the first being indistinguishable externally or represented by a slight bump, and in having the first toe hidden (Walker, 1973; Nelson, 1975). Similar though not so extreme tendencies appear in some *Chiasmocleis*, with individual variation recorded (Nelson, 1975). *Adelastes*, like other genera, has the normal complement of digits.

In its external morphology *Adelastes* is a rather generalized frog with no unique features and none other than its relative slenderness of body that sets it much apart from other American microhylid genera.

OSTEOLOGY

PECTORAL GIRDLE: The ventral elements of the pectoral girdle are important in generic assignment in the Microhylidae. The principal characters used involve the size and shape of the clavicles and procoracoid cartilages or their absence. The chief structural units of the ventral girdle, the coracoid bones,

always are present and well developed. Likewise, there is a cartilaginous sternal plate, sometimes with the style partly calcified.

American microhylids run the gamut of microhylid girdles, from those with well-developed clavicles and procoracoids to those lacking any trace of these elements. Three monotypic South American genera—*Dermatonotus*, *Otophryne*, and *Stereocyclops*, along with the Middle American *Hypopachus*, which has two species—have clavicles that reach from the glenoid region almost to the midline. Eight genera have small clavicles, generally one-half or less of the length of the coracoids, that fall far short of the glenoid region: *Arcovomer*, *Chiasmocleis* (fig. 8B), *Dasylops*,² *Elachistocleis* (fig. 8C, D), *Hamptophryne* (fig. 8A), *Hyophryne*, *Relictivomer*,³ and *Syncope*. South American *Elachistocleis bicolor* and *E. ovalis* (fig. 8D) have the procoracoids restricted to the medial ends of the clavicles, whereas a Pana-

² Bokermann's (1952, fig. 15) illustration of *Hypopachus* (= *Dasylops*) *schirchi* shows strong, curved clavicles extending to the distal ends of the coracoids, whereas Carvalho (1954, fig. 6) shows shorter bones terminating well short of the scapula. My dissection agrees with Carvalho in the extent of the clavicles, though the procoracoid appears to be more extensive than he illustrates. What appears to be a strong ligament attaches the lateral end of the clavicle to the glenoid region.

³ Carvalho (1954, pp. 13–14) erected the genus *Relictivomer* to accommodate *Hypopachus pearsei* Ruthven (1914) from Fundación, Colombia, a species that Parker (1934) had treated as a synonym of *Elachistocleis ovalis*. Carvalho differentiated *Relictivomer* from *Elachistocleis* on the basis of "the presence of the posterior part of the prevomer, the shape of the snout, and coloration," but did not elaborate. Some authors writing since Carvalho have accepted *Relictivomer* reluctantly (Cochran and Goin, 1970) or have rejected it implicitly by treating *pearsei* as an *Elachistocleis* (Kenny, 1969). Exceptions are Busack (1966) and Savage (1966), who referred Panamanian frogs to *Relictivomer* without comment, and Nelson (1985, pp. 378, 379, 390), who discussed the confused taxonomy of *Elachistocleis* and *Relictivomer* and included both genera in a checklist as a way of "avoiding prematurely resynonymizing any of the forms." Nelson included Panama within the ranges of both *Relictivomer pearsei* and *Elachistocleis ovalis*. I refer to my Panamanian specimen as *Elachistocleis* sp. in order to distinguish it from the South American *E. bicolor* and *E. ovalis* also discussed, and discuss *Relictivomer* only in terms of Carvalho's original description.

manian *Elachistocleis* sp. (fig. 8C) has the procoracoids coextensive with the clavicles. In five genera of South America (and in the Middle and North American *Gastrophryne*), clavicles and procoracoids are lacking: *Adelastes* (fig. 9), *Ctenophryne*, *Glossostoma*, *Myersiella*, and *Synapturanus*.

The primitive girdle, as seen in the out-group *Rana*, includes firmisternal coracoids, long clavicles that reach from the glenoid region of the scapula almost to the midline of the girdle, and extensive procoracoid cartilages. Reduction and loss of the clavicles and procoracoids constitute an obvious progressive derivation. Though the polarity is clear, the character's usefulness is seriously compromised by homoplasy. Reduction or loss of elements occurs not only in several American genera, but also in some members of almost all microhylid subfamilies. I have kept this in mind while incorporating the nature of the pectoral girdle into my phylogenetic scheme.

MAXILLARY ARCH: In some genera the posterior end of the maxilla is in firm contact with the quadratojugal, whereas in others the contact may be tenuous, or the bones may be separated with only a ligamentous connection. South American genera with a firm connection are *Ctenophryne*, *Dermatonotus*, *Glossostoma*, *Otophryne*, and *Stereocyclops*. In *Hamptophryne* the bones are thin and barely in contact. With respect to the unique, immature specimen of *Hyophryne*, Carvalho (1954, p. 5) stated "quadratojugal in contact with maxillary." These bones also contact in the North and Middle American *Gastrophryne* and *Hypopachus*. The remainder of the American genera—*Adelastes*, *Arcovomer*, *Chiasmocleis*, *Dasylops*, *Elachistocleis*, *Myersiella*, *Relictivomer*, *Synapturanus*, and *Syncope* have the maxillary arch incomplete, though not every species of these genera has been examined by me or described in the literature. Walker (1973, table 1) indicated a complete arch for *Synapturanus*, whereas Carvalho (1954) reported the bones not in contact. My cleared and stained specimen of *S. mirandaribeiroi* agrees with Carvalho's description.

Firm contact presumably is the primitive condition. The primitive and derived conditions also occur in microhylids phyloge-

netically remote from the American species. I recognize three states, the intermediate known only in *Hamptophryne*.

Variation in the premaxilla involves the degree to which the alary process tips forward and whether the shelf is more or less indented (notched) on its posterior margin. These characters correlate with the degree of elongation of the snout: elongate snouts are supported by the forward tilting alary processes and have little or no emargination of the premaxillary shelf. These conditions obtain in *Elachistocleis* (fig. 10F, G), *Myersiella* (Carvalho, 1954, fig. 7), *Relictivomer*,⁴ and *Synapturanus* (fig. 10H; Carvalho, 1954, fig. 8). Much less extreme conditions—vertical to slightly forward sloping alary processes, deeply to shallowly notched shelf—occur in *Stereocyclops* (Carvalho, 1948, fig. 1), *Otophryne* (examined in X-ray), *Adelastes* (fig. 10E), *Arcovomer* (Carvalho, 1954, fig. 3), *Dermatonotus* (Carvalho, 1948, fig. 1a), *Chiasmocleis* (fig. 10D; Walker and Duellman, 1974, fig. 3), *Ctenophryne* (fig. 10B), *Glossostoma* (fig. 10A), *Hamptophryne* (fig. 10C), and *Syncope* (Walker, 1973, fig. 2). I have not examined appropriate material of *Dasylops*, which Walker (1973, table 1) indicated has a notched premaxillary shelf.

Having the processes point forward is the derived condition and is not confined to these three microhylid genera. *Choerophryne* of New Guinea (Genyophryinae), with its greatly elongate snout, is a bizarre example (Menzies and Tyler, 1977). Because of the close association between orientation of the processes and degree of notching of the shelf, I treat the condition of the premaxilla as a single character with two states.

PALATAL REGION: The bones of the anterior palatal region vary among microhylids in number, size, and shape, and are important in generic definition. Unfortunately, homologies are not always clear, and individual variation is almost an unknown quantity. The

⁴ Walker (1973, table 1) included *Elachistocleis* and the questionably valid *Relictivomer* among genera with a notched premaxillary shelf. However, my three cleared and stained specimens (two South American and a Panamanian *Elachistocleis*) show little or no trace of emargination, and it would be surprising if *Relictivomer* differed.

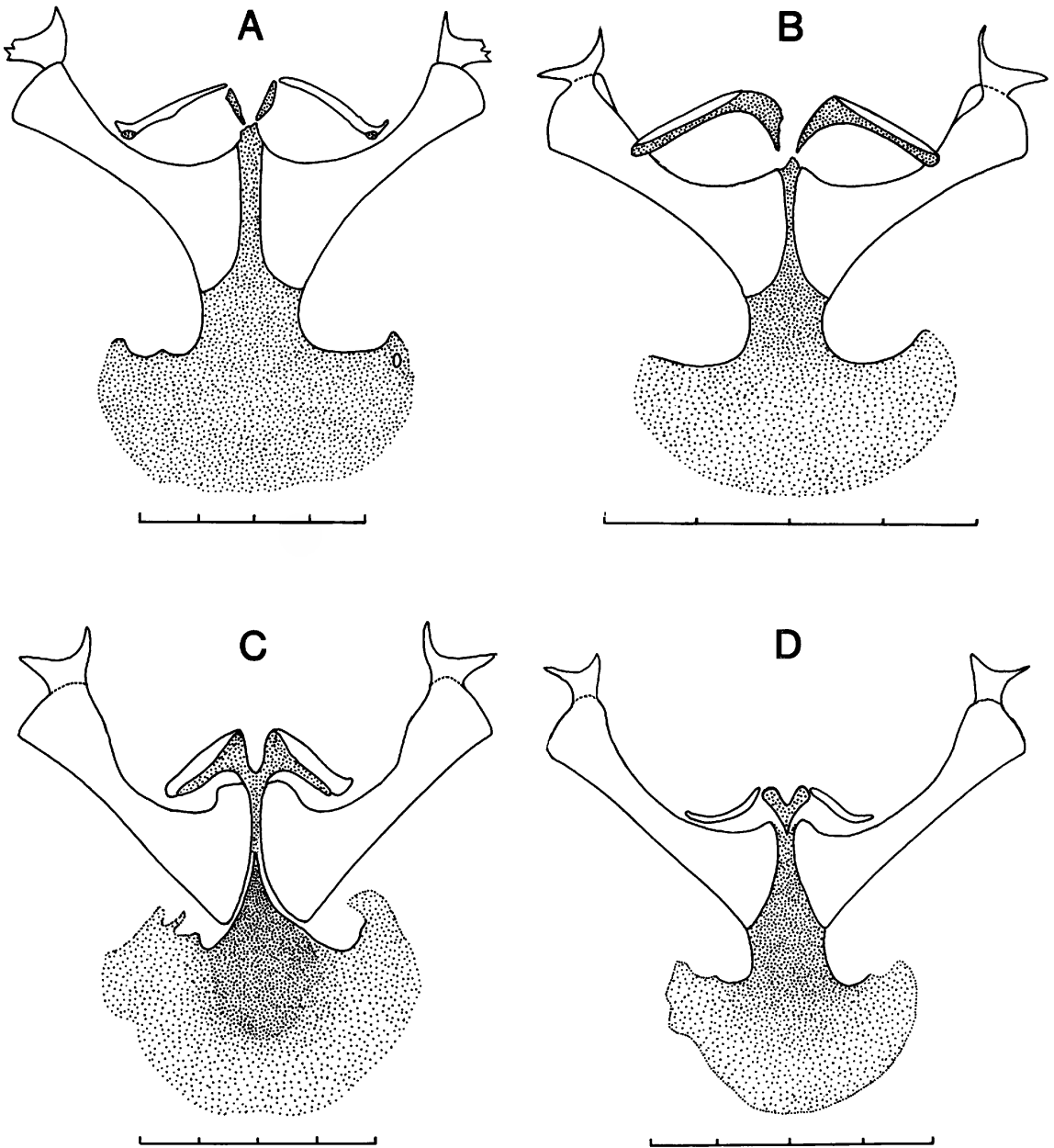


Fig. 8. Ventral elements of pectoral girdle of three genera of microhylid frogs. **A.** *Hamptophryne boliviana*, AMNH 115771. **B.** *Chiasmocleis albopunctata*, AMNH 79213. **C.** *Elachistocleis* sp., AMNH 69881. **D.** *Elachistocleis ovalis*, AMNH 113281. Stippled areas are cartilage, with denser stippling indicating some calcification; clear areas are bone. Irregular structures at distal ends of coracoids are scapulae; only terminal parts shown. Scale lines marked in mm.

bones concerned are the prevomers (vomeres of some authors), palatines, and sphenethmoid, with the parasphenoid sometimes marginally involved.

Parker (1934, p. 3) considered the primi-

tive form of the prevomer to be "that of a large, almost horseshoe-shaped plate which nearly surrounds the choana and overlies the palatal region . . ." Judged from descriptions and illustrations in the literature and from

specimens I have examined, no American species approaches this condition. The prevomer may be separated into anterior and posterior parts or reduced to an anterior part alone. The palatine is well defined in a few American species, but in others its presence is questionable or it clearly is absent. The sphenethmoid may expand laterally to border the internal nares posteriorly. In such cases it may be impossible to know whether the bone is sphenethmoid alone or incorporates palatine and posterior prevomer.

Stereocyclops incrassatus, *Glossostoma aequatoriale*, and *Hyophryne histrio* each possess a full complement of palatal bones. In the first (monotypic) genus (Carvalho, 1948, fig. 1) the anterior prevomers are free of the elongate posterior prevomers which underlie the medial half of the palatines. *Glossostoma aequatoriale* has prevomers that nearly surround the internal nares (fig. 10A). Lying ventral to the sphenethmoid is an elongate, narrow element apparently composed of two bones (posterior prevomer and palatine?), sutured near the lateral end. The subdivision into two parts is apparent on both sides of one specimen and on one side of another. I have not examined the other species of this genus, *G. aterrimum*, nor have I examined *Hyophryne*, for which Carvalho (1954, p. 4) described conditions much like those in *Stereocyclops*.

Arcovomer passarellii is peculiar in having a single posterior prevomer (so identified by Carvalho, 1954) curving across the posterior palatal region. The anterior prevomer is small and no palatine is identified (Carvalho, 1954, fig. 3).

In most South American genera the palatal elements are greatly reduced, with anterior prevomers not contacting other bones, no discrete posterior prevomers or palatines evident, and the choana bordered posteriorly by cartilage or by the ossified sphenethmoid: *Chiasmocleis* (fig. 10D; Walker and Duellman, 1974, fig. 3)⁵; *Ctenophryne* (fig. 10B); *Dermatonotus* (Carvalho, 1948, fig. 1a);

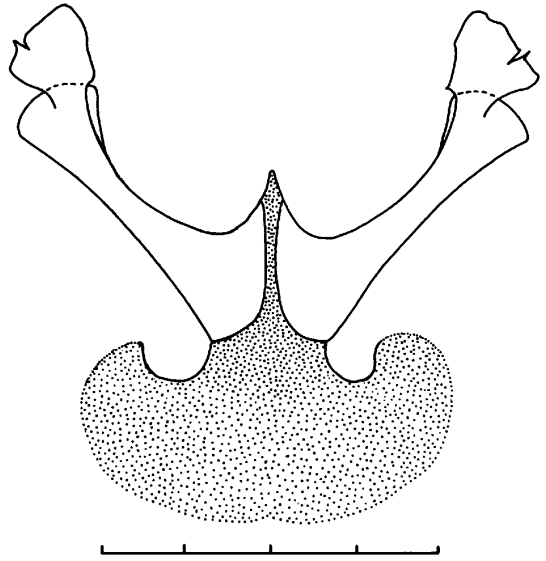


Fig. 9. Ventral elements of pectoral girdle of *Adelastes hylonomos* (AMNH 123697). Cartilage is stippled, bone clear, scapulae as in figure 8. Scale line marked in mm.

Elachistocleis (fig. 10F, G); *Myersiella* (Carvalho, 1954, fig. 7); *Syncope* (Walker, 1973, fig. 2).⁶ The North and Middle American genera *Gastrophryne* and *Hypopachus* have this condition too. The palate of *Dasypops* has not been described, though Carvalho's (1954) comparisons with *Dermatonotus* and *Hypopachus* imply similar palatal morphology.

Hamptophryne differs from the foregoing genera only in possessing a tiny sliver of bone, identified by Carvalho (1954, p. 4) as posterior prevomer, lying on (Carvalho, 1954, fig. 8) or just medial to the anteromedial edge of the sphenethmoid (fig. 10C). *Relictivomer*, as illustrated and briefly described by Carvalho (1954, p. 13, fig. 5), has essentially the same palate as *Hamptophryne*. Inasmuch as frogs of this sort from Panama have been referred to *Relictivomer*, it is noteworthy that an *Elachistocleis* from Panama (fig. 10F) lacks the tiny posterior prevomers of *Relictivomer*.

Synapturanus is unique among microhylids in having an ossified extension of the

⁵ Walker and Duellman (1974, p. 3) stated "posterior prevomer . . . fused to sphenethmoid medially" in *C. anatis* but do not say why the uniform bone illustrated represents fusion rather than loss of the posterior prevomer.

⁶ Walker (1973, p. 2) stated "posterior prevomer well developed, medially fused with ethmoid." As in *C. anatis*, the case for fusion rather than loss of the posterior prevomer is not made.

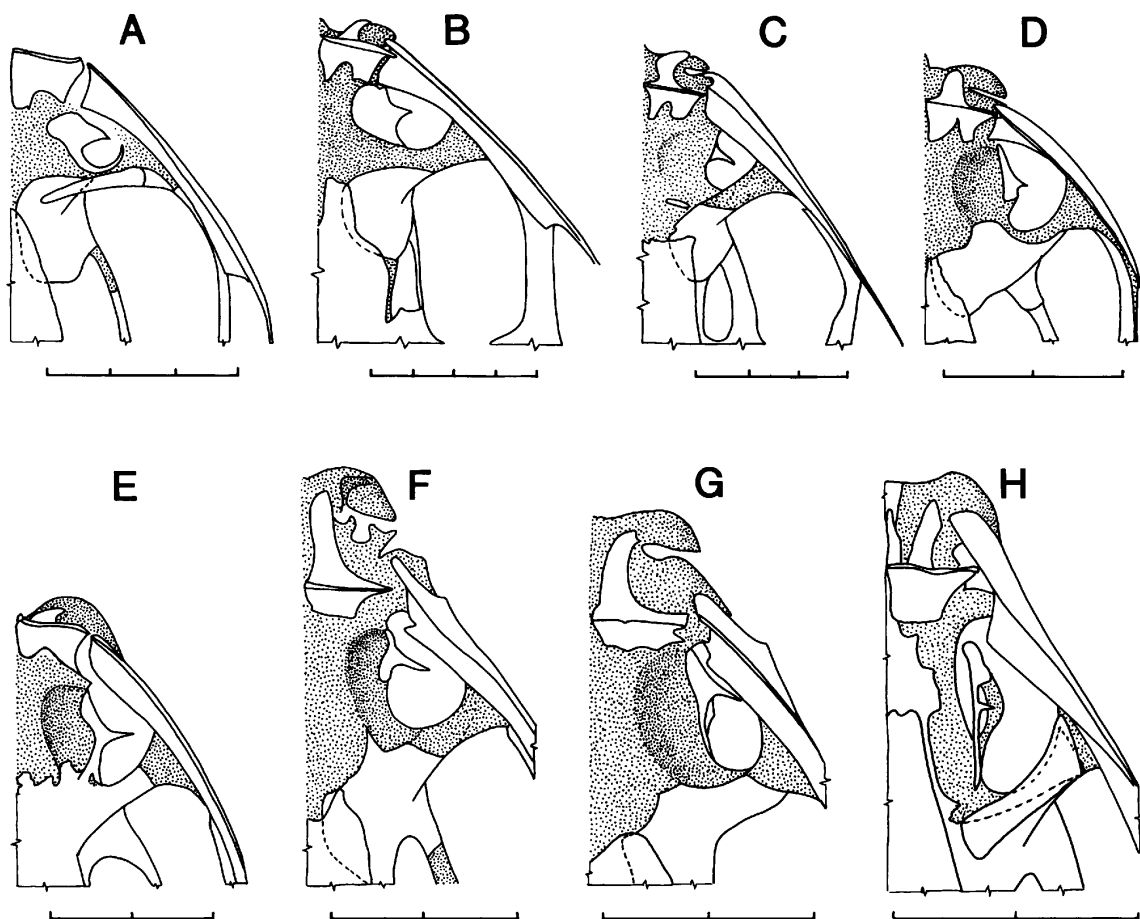


Fig. 10. Ventral view of left palatal region of seven genera of microhylid frogs. A. *Glossostoma aequatoriale*, AMNH 17613. B. *Ctenophryne geayi*, AMNH 42663. C. *Hamptophryne boliviana*, AMNH 115771. D. *Chiasmocleis albopunctata*, AMNH 79213. E. *Adelastes hylonomos*, AMNH 123697. F. *Elachistocleis* sp., AMNH 69881. G. *Elachistocleis ovalis*, AMNH 113281. H. *Synapturanus mirandaribeiroi*, AMNH 90936. Cartilage is stippled, bone clear. Scale lines marked in mm.

sphenethmoid that reaches into the snout anterior to the palatal shelves of the premaxillae (fig. 10H; Carvalho, 1954, fig. 8). In other respects Carvalho's (1954) description and illustration of "*Synapturanus microps*" (= *S. mirandaribeiroi*, fide Nelson and Lescure, 1975) differ from my specimen of that species. Carvalho (1954, pp. 17–18) stated "Prevomer divided, posterior part absent, anterior part fused with ethmoids and parasphenoid to form a single bony element . . . No palatine." In my specimen (fig. 10H, a paratype of *mirandaribeiroi*) the prevomer is free, not contacting any other bone; the outline of the parasphenoid is distinct, unobscured by fusion; there is a large palatine, distinguished

both in outline and in texture from the overlying sphenethmoid. Reasons for the differences between the two specimens are unknown. They are of a sort that could be associated with ontogenetic change, though my specimen (SV 30.0 mm, female) is almost as large as the adult female holotype (SV 32.9 mm, Nelson and Lescure, 1975) and the specimen that Carvalho examined (SV 31.8 mm, female).⁷

The palatal region of *Adelastes* in some

⁷ Carvalho's specimen (formerly AMNH 53204, now Museu Nacional do Rio de Janeiro no. 4256) from Shudikar Wau, Guyana, kindly was measured for me by Ulisses Caramaschi.

respects resembles that of *Synapturanus* as described by Carvalho: the prevomer and sphenethmoid are fused, it is impossible to distinguish the parasphenoid anteriorly from the ethmoid (which, as in *Synapturanus*, lacks the usual ventral gap), and there is no palatine. There is, however, no indication of the anterior prolongation of the sphenethmoid seen in the sharper snouted *Synapturanus*.

The possession of a complete suite of palatal bones must be taken as the primitive condition. Parker (1931) discussed what he considered parallel reductions in the prevomers of Malagasy and Indo-Australian microhylids, with separation of anterior and posterior parts being an early stage in the process. He earlier (1928) presented what appear to be successive steps in the reduction of the palatine and its replacement by the sphenethmoid in species of the Asian genus *Microhyla*, and later (1934, p. 4) stated that the palatine, "like the post-choanal portion of the prevomer, from which it frequently cannot be distinguished, is often reduced or absent." In some cases both anterior and posterior parts of the prevomers evidently exist in American microhylids, but in others it is not clear which bone or bones make up the postchoanal palatal elements. Although the various reductions, fusions, and deletions are derived states, it is by no means certain where the synapomorphies lie. The several derived states I recognize (table 2) are not readily arranged among themselves.

HYOID APPARATUS: No microhylid other than *Adelastes* is known to have a parahyoid bone. Apart from this, I find nothing particularly distinctive in the hyoids of the several genera examined.

VERTEBRAL COLUMN: Most genera of American microhylids, *Adelastes* included, have eight presacral vertebrae with the eighth amphicoelous—the diplasiocoelous condition. Exceptions among those with eight presacral vertebrae are *Myersiella*, with all presacrals procoelous (Carvalho, 1954; confirmed by me in two X-rayed specimens), and *Chiasmocleis*, in which genus both procoelous and diplasiocoelous conditions occur (Walker and Duellman, 1974). *Arcovomer* is said to be diplasiocoelous (Carvalho, 1954). My specimen of *Arcovomer*, as seen in X-ray, is neither clearly diplasiocoelous nor procoe-

lous, but appears to have a free intervertebral ball. *Syncope* is unique in having only seven presacrals, all procoelous (Walker, 1973; Nelson, 1975).

Fusion of the first two vertebrae characterizes *Syncope*, though the extent of ankylosis varies. Similar fusion, possibly as individual variation, occurs in *Elachistocleis*. Among three specimens, a *bicolor* has these bones fused whereas they are free in an *ovalis* and in an unassigned Panamanian specimen.

Whether vertebrae overlap dorsally (the imbricate condition) or are separated by gaps can be used as a character in assessing relationships. My material is inadequate for a thorough survey of the genera, but in several specimens I examined the vertebrae are non-imbricate except for the first two or three. I observed this condition in *Adelastes*, *Chiasmocleis*, *Elachistocleis* (*bicolor* and sp.), and *Gastrophryne*. The vertebrae are marginally nonimbricate posteriorly in *Hamptophryne* and narrowly imbricate in *Ctenophryne* and *Elachistocleis ovalis*. *Synapturanus mirandaripei* shows an extreme nonimbricate condition. Individual, possibly ontogenetic variation can occur: One specimen of *Glossostoma aequatoriale* (female, 36.6 mm SV) has strongly imbricate vertebrae whereas another (male, 29.7 mm SV) has slight gaps. The imbricate condition may be primitive, but individual variation and paucity of material preclude effective use of this character.

The sacral vertebrae of all genera I examined or that are illustrated in the literature (*Hyophryne* is unknown) have expanded diapophyses and articulate with the coccyx through paired condyles; no instances of sacrococcygeal fusion were found (fig. 11). Nelson and Lescure (1975, p. 391) modified Carvalho's (1954) diagnosis of *Myersiella* to include "coccyx articulating with sacrum by a single condyle," based on a radiograph of the holotype of this monotypic genus. If true, this would make *Myersiella* unique among American microhylids and probably unique in the family (Parker, 1934, p. 5), but X-ray photographs of my two specimens clearly show double condyles. It would be worthwhile to establish if *Myersiella* is indeed polymorphic for this feature or if there is some other explanation. There is precedent for such

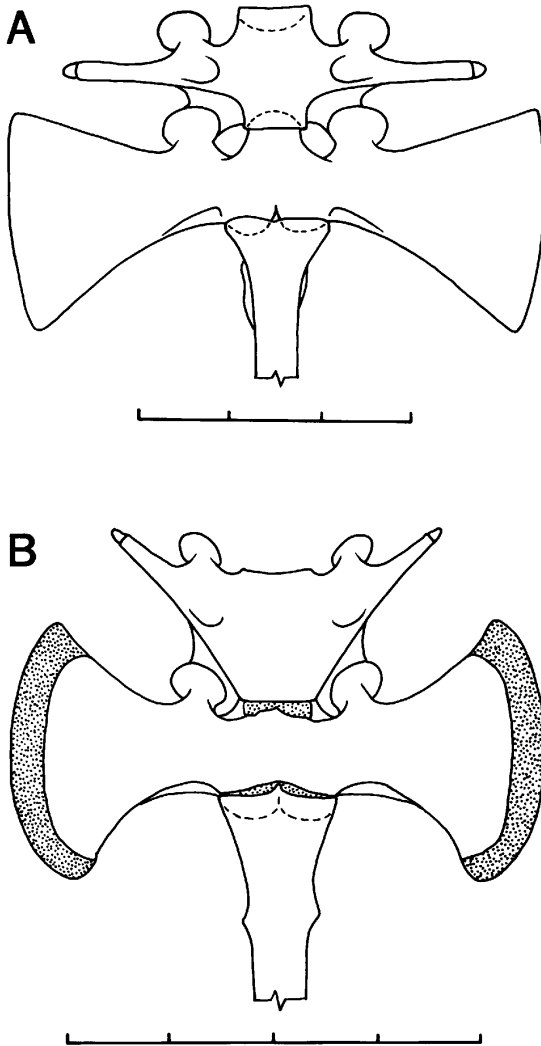


Fig. 11. Dorsal view of presacral and sacral vertebrae and basal region of coccyx. A. *Synapturanus mirandaribeiroi*, AMNH 90936. B. *Adelastes hylonomos*, AMNH 123697. Stippled areas are cartilage (not adequately stained in *Synapturanus*), clear areas bone. Scale lines marked in mm.

variation in the bufonid genus *Nectophrynoides* (Grandison, 1978, p. 145).

Most genera lack coccygeal diapophyses, though rarely a slight projection is present, often only unilaterally. The principal exception is *Syncope*, in which the processes range from vestigial to well developed (Walker, 1973; Nelson, 1975). X-ray photographs of specimens of *Dasylops* and *Otophryne* show

what appear to be very weak projections. *Myersiella* evidently is variable: one X-rayed specimen apparently has no processes while another has a slight unilateral shelf. Walker (1973, table 1) indicated presence, Carvalho (1954) reported vestiges, and Nelson and Lescure (1975) recorded presence as seen in a radiograph of the holotype. *Hyophryne* has not been described.

The vertebral column is of little use in inferring intergeneric relationships. The derived character of fused vertebrae in *Syncope* is an autapomorphy, assuming that the fusion observed in one specimen of *Elachistocleis* is an individual anomaly. Procoely in one species of *Chiasmocleis* (but not in another species I examined, nor was it reported by Carvalho, 1954) is unlikely to be homologous with that in the otherwise distinctive *Myersiella*. Procoely in *Syncope* is a consequence of shifting the sacral function forward to the eighth vertebra, so that the normally procoelous seventh is the presacral, a condition not homologous with the procoely of *Chiasmocleis anatis* or *Myersiella*. Similarly, the presence of vestigial diapophyses on the coccyx of *Syncope* results from incorporation of the ninth vertebra into the coccyx and is thus not a primitive character. Accordingly, three characters of *Syncope*—vertebral number, procoely, and coccygeal diapophyses—are, for purposes of analysis, a single autapomorphy.

APPENDAGES: Differences in the bones of the appendages of American microhylids involve shape of the terminal phalanges of fingers and toes and the loss of phalanges in the foot. In *Syncope* the phalangeal formula of the foot is 1-2-3-4-3 (Walker, 1973), compared with the usual 2-3-3-4-3 seen in all other genera.

In most genera the tips of the terminal phalanges are not or only slightly differentiated, ranging from narrow and rounded in *Adelastes* to slightly bulbous in *Ctenophryne* and *Stereocyclops*. *Hamptophryne* differs in that the terminal phalanges of the toes are slightly bilobed, whereas *Arcovomer* has both finger and toe tips T-shaped. The conditions in *Hamptophryne* and *Arcovomer* probably are apomorphic, but whether the bilobed phalanges are precursors of T-shaped ones is uncertain.

CHROMOSOMES

Karyotypic data are known for 12 species in 10 of the 18 nominal genera of American microhylids (Bogart and Nelson, 1976; Bogart et al., 1976). Unfortunately, *Adelastes* is among the unknown.

Most known American species have a diploid number of 22, one (the only species of *Chiasmocleis* karyotyped) has 24, whereas *Glossostoma aequatoriale* (*G. aterrimum* has not been studied) and the monotypic *Otophryne* have 26. Data for Old World microhylids are far from complete, but the summary by Bogart and Nelson (1976) recorded numbers of 24, 26, and 28 in representatives of Asiatic microhylines, 24 in African brevicipitines, and 26 in African phrynomerines and New Guinean asterophryines and genyophrynines. Blommers-Schlösser (1976) added Malagasy Dyscophyinae and Cophylinae to those with a diploid number of 26.

Bogart and Nelson (1976) suggested that the 26-chromosome karyotype, found in many families of frogs, is primitive within the microhylid context, and that $2n = 22$ is a derived condition. That the 22 chromosome karyotype is unique to American species among microhylids is suggestive of the monophyly of at least part of the New World fauna.

VOCALIZATIONS

A number of authors have published verbal descriptions of the advertisement calls of American microhylid frogs, but only Nelson (1973) dealt objectively with a wide range of species (American and Asiatic) in a phylogenetic context, tabulating the characteristics of calls of many species and providing audiospectrograms. Nelson (1973, pp. 164–165) separated the calls of New World microhylines into “three discrete groups: bleats, single whistles, and trilled calls.” The first group includes the genera *Dermatonotus*, *Hypopachus*, *Gastrophryne*, and *Elachistocleis*, which have a single prolonged note with dominance poorly defined among several harmonics present. *Glossostoma aterrimum* and *Hampophryne* produce similar but shorter calls with more harmonics. *Synapturanus* (true also of at least one of the two species described since Nelson’s report; Pyburn, 1975),

Myersiella, and *Arcovomer* have simple whistles, whereas *Dasypops*, *Ctenophryne*, *Chiasmocleis*, and *Stereocyclops* have calls that are “distinctly trilled or slowly pulsed” (Nelson, 1973, p. 168). Wassersug and Pyburn (ms.) characterize the advertisement call of *Otophryne* as “a sequence of short, raspy notes . . . with a pause of several seconds between note sequences” and furnish a detailed analysis. With respect to *Syncope*, Duellman (1978, p. 192) wrote: “No call was associated with [*S. antenori*] The absence of vocal slits in adult males perhaps is indicative that this small frog is mute.” Some frogs without vocal slits (or sacs—the two go together) do call, however, so we cannot assume that *Syncope* is mute.

The distinction between “bleats” and “trilled or slowly pulsed” calls is not a fundamental one. “Bleats” are rapidly pulsed, single-note calls of short to long duration. “Trilled” calls differ mainly in their slower pulse rate, whereas Nelson applied the term “slowly pulsed” to calls that consist of a series of short notes that are on close inspection rapidly pulsed. For example, audiospectrograms of calls of *Chiasmocleis bicegoi* and *C. leucosticta* made with the 300 Hz filter, which provides better temporal resolution than Nelson’s spectrograms (1973, fig. 4), made with the 45 Hz filter,⁸ reveal pulse rates (within each note) of about 180 and 75 pulses per second, respectively.

I suggest that the calls Nelson studied might be categorized as single, pulsed notes, pulsed notes in series, and single unpulsed whistles. Pulsed notes in series may be derived from single pulsed notes (increased complexity), whereas single unpulsed whistles may represent another sort of derivation in which a high-frequency fundamental rather than one or more harmonics of a lower-frequency fundamental is dominant.

The call of *Adelastes* is not clearly pulsed or well tuned, and therefore fits neither the broader category of pulsed calls nor the distinctive single-whistle group. It appears to be unique among calls of American microhylids. There is similarity between the call of *Adelastes* and that of *Otophryne*, especially

⁸ Copies of some of Dr. Nelson’s recordings are in the AMNH Department of Herpetology tape library.

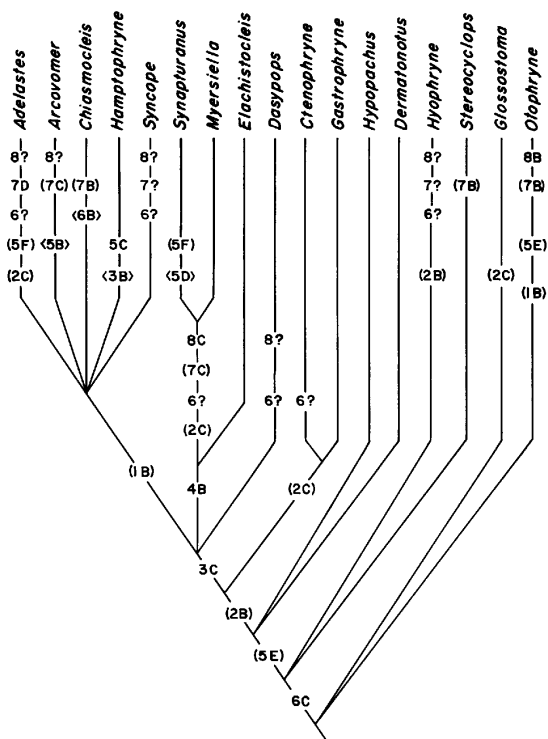


Fig. 12. A hypothesis of relationships among American microhylid frog genera. See tables 2 and 3 for the character states and their distribution among the genera. States shown in parentheses appear independently in more than one branch of the cladogram; brackets indicate reversals, and unknown states are questioned.

in that each consists of a brief series of short, rather harsh, notes. *Otophryne*, however, shows distinct harmonic bands (interval about 800 Hz), and I tentatively include it in the category of pulsed notes in series.

LARVAE AND LIFE HISTORY

Nothing is known of the breeding habits of *Adelastes*, but some potentially useful information is available for other species. Typical microhylid breeding involves pigmented eggs deposited in water that develop into a morphologically distinctive type of tadpole (Orton, 1953) known only in the Microhylidae. At least eight genera of American microhylids have larvae of this sort (larvae of others in addition to *Adelastes* are undescribed). The larvae of *Otophryne* hatch from unpigmented eggs and have numerous mor-

phological peculiarities (Pyburn, 1980; Wassersug and Pyburn, ms.). *Glossostoma* is said to have a larva more similar to Asiatic forms than to most other American forms (Nelson, 1969), but supporting data have not been published.

Myersiella (Izecksohn and Jim, 1971) and *Synapturanus* (Pyburn, 1975, 1977) lay their eggs in nests in the forest floor. The nonfeeding larvae hatch at a late stage of development and undergo transformation in the nest. Similar or more extreme deemphasis of the larval stage occurs in distantly related microhylids in other parts of the world. Duellman (1978) suggested that *Syncope* may have direct development in terrestrial sites, based on the small complement and relatively large size of its eggs. The eggs, however, are heavily pigmented (Walker, 1973), a feature associated with aquatic breeding.

Aquatic breeding with typical microhylid larvae is the primitive condition (though the larva is derived compared with those of other families), whereas the peculiar larva of *Otophryne* and terrestrial breeding without an aquatic larval stage in two other genera are derived states.

INTERGENERIC RELATIONSHIPS

The act of describing a new genus carries with it obligations to defend the need for burdening taxonomy with yet another entry (especially in the case of monotypic genera) and to assess the phylogenetic position of the new taxon relative to other congeneric genera. As for the first, it is sufficient that the unique characters of the hyoid and possibly of the call, together with other characters combined in a unique way, make it impossible to accommodate the new species within any described genus without unreasonably expanding and diluting the generic definition.

The matter of intergeneric relationships is more difficult to handle, both because of incomplete data and of alternative of conflicting interpretations of data. A full-scale study of the American microhylid genera is well beyond the scope of this paper. What I have done is survey the literature on the subject, examine osteological and preserved material of most of the genera, and select certain osteological and other characters for cladistic analysis.

TABLE 2
Characters for Analysis of Generic Relationships^a

| | |
|--|--|
| 1A. Occipital fold present. | 1B. Occipital fold lacking. |
| 2A. Clavicles long, spanning almost all of distance between glenoid and midline of girdle. | 2B. Clavicles reduced, about one-half to one-third length of coracoids, not reaching glenoid region. |
| 3A. Quadratojugal and maxilla in firm bony contact. | 2C. Clavicles and procoracoids absent. |
| 4A. Alary process of premaxilla vertical or sloping only slightly forward; shelf of premaxilla moderately to deeply notched. | 3B. Quadratojugal and maxilla in tenuous contact (<i>Hamptophryne</i>). |
| 5A. Anterior and posterior prevomers and palatines distinct from one another, unfused. | 3C. Quadratojugal and maxilla separate. |
| | 4B. Alary process tilted forward; shelf not or scarcely notched. |
| 6A. $2n = 26$ chromosomes. | 5B. Anterior prevomers and a single, transverse posterior prevomer; no palatines (<i>Arcovomer</i>). |
| 7A. Call a single pulsed note | 5C. Anterior prevomers and tiny posterior prevomers present; no palatines (<i>Hamptophryne</i>). |
| 8A. Larva aquatic, free living, of typical microhylid morphology. | 5D. Anterior prevomers and large palatines present; no posterior prevomers (<i>Synapturanus</i> , in part). |
| | 5E. Anterior prevomers present, posterior and palatines absent or not distinguished from sphenethmoid. |
| | 5F. As in E, but anterior prevomers and parasphenoid fused with sphenethmoid. |
| | 6B. $2n = 24$ chromosomes. |
| | 6C. $2n = 22$ chromosomes. |
| | 7B. Call a series of pulsed notes. |
| | 7C. Call a one-note whistle. |
| | 7D. Call a harsh, repeated chirp (<i>Adelastes</i>). |
| | 8B. Larva aquatic-fossorial with elongate teeth and long spiracular tube (<i>Otophryne</i>). |
| | 8C. Larva hatches at late stage of development, metamorphoses in terrestrial nest. |

^a Character states in the left column (A) are considered primitive; those on the right are derived, but their order (B–F) does not necessarily imply a primitive–derived sequence. For example, 8B and 8C are thought to be independently derived from 8A, whereas 2A → 2B → 2C possibly form a series (see text). Where a genus is given, the state is known only from that genus.

PREVIOUS INVESTIGATIONS: In his monograph of the Microhylidae, Parker (1934) presented a conservative interpretation of American microhylids, treating many New World species as members of the Asiatic *Microhyla* and recognizing only six additional genera. This view prevailed in large measure until the appearance of Carvalho's (1954) "preliminary" (but unfortunately, only) synopsis of American genera. Using mainly osteological characters, Carvalho redefined, resurrected, and described taxa, recognizing 15 genera—more than twice Parker's total. Subsequent workers have come to follow Carvalho's arrangement wholly or in large part.

Carvalho (1954) presented no inclusive phylogenetic scheme, but remarked on relationships among and between genera, citing characters given significance. Most discus-

sion of intergeneric relationships has come from C. E. Nelson and associates: Nelson and Cuellar, 1968 (larvae); Nelson, 1969 (abstract of summary discussion); Nelson, 1973 (vocalizations); Nelson and Guttman, 1973 (serum proteins); Bogart and Nelson, 1976 (karyotypes). In addition, Walker (1973) discussed the relationships of the new genus *Syncope*.

ANALYSIS OF CHARACTERS

From the features discussed in the foregoing section comparing the genera, I have selected eight characters and defined 26 states for use in analyzing relationships. The characters and states are presented in table 2 and their distribution among the genera appears in table 3. The cladogram developed from these characters (fig. 12) reflects the high de-

TABLE 3
Distribution of Character States Among American Microhylid Genera^a

| Genera | Characters | | | | | | | |
|-----------------------|------------|---|--------|---|------|---|---|---|
| | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 |
| <i>Adelastes</i> | B | C | C | A | F | ? | D | ? |
| <i>Arcovomer</i> | B | B | C | A | B | C | C | ? |
| <i>Chiasmocleis</i> | B | B | C | A | E | B | B | A |
| <i>Ctenophryne</i> | A | C | A | A | E | ? | A | A |
| <i>Dasylops</i> | A | B | C | A | E? | ? | A | ? |
| <i>Dermatonotus</i> | A | A | A | A | E | C | A | A |
| <i>Elachistocleis</i> | A | B | C | B | E | C | A | A |
| <i>Gastrophryne</i> | A | C | A | A | E | C | A | A |
| <i>Glossostoma</i> | A | C | A | A | A | A | A | A |
| <i>Hamptophryne</i> | B | B | B | A | C | C | A | A |
| <i>Hyophryne</i> | A | B | A | A | A | ? | ? | ? |
| <i>Hypopachus</i> | A | A | A | A | E | C | A | A |
| <i>Myersiella</i> | A | C | C | B | E | ? | C | C |
| <i>Otophryne</i> | B | A | A | A | E | A | B | B |
| <i>Stereocyclops</i> | A | A | A | A | A | C | B | A |
| <i>Synapturanus</i> | A | C | C (A?) | B | D, F | ? | C | C |
| <i>Syncope</i> | B | B | C | A | E | ? | ? | ? |

^a See Table 2 for definition of character states.

gree of homoplasy seen in microhylid frogs, a situation that continues to plague attempts at inferring relationships and establishing a stable taxonomy.

I have excluded *Relictivomer* from this discussion because of inadequacy of data and the questionable validity of the taxon. Presumably it would cluster with *Elachistocleis*.

Clearly *Glossostoma* is the most primitive genus, having only one derived character state, loss of the clavicles and procoracoids. Among characters not included in the diagram, it appears primitive in its foot structure (webbed with rounded toe tips) and possibly in its larva, which Nelson (1969) found more comparable with Asiatic than with American microhylines.

Setting aside *Otophryne* for the present, I have grouped the remaining genera as characterized by having $2n = 22$ chromosomes (character state 6C). This character state is true for seven of the genera, unknown in seven, and not true in the only species of *Chiasmocleis* karyotyped ($2n = 24$). Because such otherwise primitive genera as *Stereocyclops*, *Dermatonotus*, and *Hypopachus* (both species) have the derived character, I think it a reasonable hypothesis that it will prove

common to those whose karyotypes are at present unknown. *Chiasmocleis* may prove variable in this respect as it has in several others. Placing *Chiasmocleis* near the base of the diagram in order to accommodate its intermediate chromosome number between the primitive $2n = 26$ and derived $2n = 22$ would create more problems than it would solve.

Hyophryne and *Stereocyclops* are similar in many respects but share no known derived character that sets them apart from other genera. Acquisition of more specimens of and nonmorphological data on *Hyophryne* (it is known only from the holotype) should help define its position.

The next branch in the cladogram, defined by fusion or loss of posterior elements of the palatal bony complex (state 5E), is perhaps the least satisfactory; yet I see no better alternative. Nine of 13 genera have state 5E and another (*Adelastes*) has a more derived state of fusion (5F). *Hamptophryne* shows vestiges of the posterior prevomers (state 5C), but other considerations place it well above the present dichotomy. *Arcovomer* has a peculiar condition (state 5B), the presence of a single transverse posterior prevomer (or palatine?). In the present scheme the freedom of this bone from fusion with the sphenethmoid constitutes a reversal, while deviation from the primitive condition of paired bones is an autapomorphy. The apparently variable condition in *Synapturanus* must be treated partly as a reversal (state 5D) and partly as an autapomorphy (5F) paralleling the condition in *Adelastes*.

Hypopachus and *Dermatonotus* are similar in most characters and were at one time considered congeneric, though the similarity owes largely to shared primitive characters.

All genera on the next highest branch of the diagram have the clavicles reduced in size (state 2B) or the more derived state (2C), clavicles lacking. These modifications of the pectoral girdle occur commonly in genera of other subfamilies, so it is not particularly bothersome that two genera on lower branches of the cladogram (*Glossostoma* and *Hyophryne*) have attained derived states independently.

Gastrophryne and *Ctenophryne* share the most reduced state of the pectoral girdle (2C) and so can conveniently be segregated on their

own branch, though it would be desirable to have a stronger synapomorphy to unite them (this state appears twice again higher up on the cladogram). That one species of *Gastrophryne* (*G. usta*) and *Hypopachus* have both inner and outer metatarsal tubercles relatively well developed, presumably a derived state, is suggestive of a closer relationship between these genera than the diagram indicates. But to accept the condition of the tubercles as a synapomorphy of *G. usta* and *Hypopachus* would require yet another independent derivation of the reduced state of the pectoral girdle as well as a reversal in all other *Gastrophryne* of the derived state of metatarsal tubercle seen in the one species and *Hypopachus*.

The next synapomorphy—loss of contact between maxilla and quadratojugal—is consistent except for *Hamptophryne*, which has a narrow contact, scored as a reversal.

Though *Dasytops* is placed here as part of a trichotomy, its reduction in head size (fig. 6D) could be considered a synapomorphy on the branch leading to *Elachistocleis*, *Myersiella*, and *Synapturanus*. That branch is one of the better defined: The three genera share a synapomorphy of the premaxillary bones (state 4B), and *Synapturanus* and *Myersiella* have in common apomorphic traits of the pectoral girdle (2C), voice (7C) and breeding habits (8C).

The remaining five genera share the lack of an occipital fold (state 1B) and have generally similar head shapes (fig. 7), but I find no characters pointing strongly to closer relationships between or among any of these five. *Adelastes* has a unique call and a derived palate that at least partly parallels that of *Synapturanus*, but its reproductive mode is unknown. *Arcovomer* has a unique palate, a call convergent with those of *Myersiella* and *Synapturanus*, and unknown reproductive mode. *Hamptophryne*, with its bilobed terminal phalanges, perhaps is more closely related to *Arcovomer* (T-shaped terminal phalanges), but otherwise is quite different. Walker (1973, p. 5) thought that "*Syncope* could not have evolved from any existing genus." He placed emphasis on two primitive characters—presence of distinct tympanum and posterior prevomer—attributed to *Syncope*. The first character does not hold up in a species of

Syncope described subsequently and the second appears to be equivocal. I suspect that when the probably polyphyletic genus *Chiasmocleis* is investigated in depth it will be possible to find a relationship with *Syncope* in that assemblage. The trend toward digital reduction in some *Chiasmocleis* may point the way.

Otophryne remains an enigma. It has a primitive karyotype but a derived palate, primitive pectoral girdle and maxillary arch but a unique, derived larva and a derived call. The head shape (fig. 6I), tympanum, and other aspects of body form also set it apart. I see no basis for considering it closely related to any other American or Asiatic genus. Wassersug and Pyburn (ms.), in a more exhaustive analysis, conclude that *Otophryne* deserves segregation in a monotypic subfamily of the Microhylidae.

PREVIOUS STATEMENTS OF RELATIONSHIPS: Nelson (1973) felt that similarities in call structure confirmed most of the intergeneric relationships suggested by Carvalho (1954) and suggested close relationships among *Gastrophryne*, *Hypopachus*, *Elachistocleis*, *Dermatonotus*, and *Glossostoma*. He commented further (1973, p. 172) that "similarities of the call of *Hamptophryne* to that of *Glossostoma* either must be regarded as convergent or the affinities of the genus must be re-evaluated." In my proposed phylogeny, this common call structure is regarded as primitive and thus is not indicative of close relationship in this suite of genera. In contrast, Nelson and I both interpret the similarities in calls of *Synapturanus* and *Myersiella* as indicating close relationship.

A difference in interpretation of call structure underlies our varied placement of some other genera. In agreement with Carvalho, Nelson grouped *Stereocyclops*, *Ctenophryne*, and *Chiasmocleis*, and suggested that *Dasytops* (placed elsewhere by Carvalho) had affinities here too. This was because of the "trilled" nature of the calls, but as I discussed above, some "trills" (*Ctenophryne*, *Dasytops*) are continuously pulsed calls, whereas others (*Stereocyclops*, *Chiasmocleis*) are pulsed calls broken up into separate notes. In my interpretation the similarities of calls of *Ctenophryne* and *Dasytops* probably indicate retention of a primitive character,

whereas the otherwise very different *Chiasmocleis* and *Stereocyclops* have attained their resemblance independently.

Bogart and Nelson (1976) emphasized the uniqueness of the 22-chromosome diploid karyotype for American genera and (p. 199) noted that "*Glossostoma* ($2n = 26$) and *Chiasmocleis* ($2n = 24$) are the most distinctive karyotypically." They further stated that "among the 22 chromosome genera, *Gastrophryne* and *Hypopachus* are very similar and *Elachistocleis* is allied to them, *Arcovomer* is similar to *Hamptophryne*, and *Stereocyclops* is most distinctive." Bogart et al. (1976, p. 210) cautioned that common possession of the primitive 26-chromosome karyotype by *Glossostoma* and *Otophryne* "should not be interpreted as evidence of close affinity." None of these conclusions conflicts with my proposed phylogenetic arrangement.

Nelson and Guttman (1973, p. 427) found serum protein patterns suggesting that "*Gastrophryne* and *Hypopachus* are closely related . . . and *Elachistocleis* is relatively close to these two genera whereas *Glossostoma* is more divergent." Again, these conclusions do not conflict with mine, but a significant contribution from biochemical systematics awaits a much broader database.

MONOPHYLY OF AMERICAN MICROHYLIDAE: My foregoing analysis assumed that the American genera constitute a monophyletic group. The frequency of the 22-chromosome karyotype among these genera and its apparent absence from Old World genera suggests that at least this large group of American forms may be monophyletic, but additional evidence from karyology and from unrelated areas—myology and biochemistry especially—is badly needed. With respect to relationships outside the Western Hemisphere, information accumulated since Parker's monograph was written has produced sufficient exceptions to his definition of the Microhylinae that a reexamination on the subfamilial level is overdue.

SKELETAL MATERIAL EXAMINED

CLEARED AND STAINED SPECIMENS: *Adelestes hylonomos*, AMNH 123697, paratype, vicinity of Neblina Base Camp, Amazonas Territory, Venezuela. *Chiasmocleis albo-*

punctata, AMNH 79213, Trinidad, Beni Prov., Bolivia. *Ctenophryne geayi*, AMNH 42663, Pampa Hermosa, Peru. *Elachistocleis bicolor*, AMNH 19890, Paraguay. *Elachistocleis ovalis* (*surinamensis*?), AMNH 113281, Churchill-Roosevelt Highway, Trinidad. *Elachistocleis* sp., AMNH 69881, 1 mi W Nueva Gorgona, Panama Prov., Panama. *Gastrophryne carolinensis*, AMNH 59517 + 2, Cove Point, Calvert Co., Maryland; AMNH 59521 + 1, Fort McClellan, Calhoun Co., Alabama; AMNH 116397, 116398, Imboden, Lawrence Co., Arkansas. *Glossostoma aequatoriale*, AMNH 17559, 17613, Cinineay, Ecuador. *Hamptophryne boliviana*, AMNH 115771, Río Ampiyacu, Estirón, Loreto, Peru. *Synapturanus mirandaribeiroi*, AMNH 90936 (paratype), Kanashen, Rupununi Dist., Guyana.

SPECIMENS EXAMINED BY X-RAY: *Arcovomer passarellii*, AMNH 79861, Horto Forestal, Itaguaí, Rio de Janeiro, Brazil. *Ctenophryne geayi*, AMNH 44787, Rio Livramento, Amazonas, Brazil; AMNH 73547, Manjuru, Amazonas, Brazil; AMNH 76183, Maues, Amazonas, Brazil. *Dasylops schirchi*, AMNH 69926, 73551, Linhares, Espírito Santo, Brazil. *Hypopachus variolosus*, AMNH 89189, 89194, 89196, 4 mi NW Jocotepec, Jalisco, Mexico. *Myersiella microps*, AMNH 79859, 79860, Tijuca, Rio de Janeiro, Brazil. *Otophryne robusta*, AMNH 71015, Kartabo, Essequibo Co., Guyana; AMNH 92114, 92115, Wacará, Vaupés, Colombia. *Stereocyclops incrassatus*, AMNH 56117, Barro Branco, Rio de Janeiro, Brazil; AMNH 73552, 73553, Linhares, Espírito Santo, Brazil.

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